Hungarian University of Agricultural and Life Sciences

INVESTIGATION OF THE FACTORS DETERMINING THE LANDSCAPE-SCALE ORGANIZATION OF FUNGAL COMMUNITIES IN GRAPEVINE (*VITIS VINIFERA*) AND IN HABITAT MOSAICS OF CULTIVATED AND SEMI-NATURAL *ROSACEAE* SPECIES

Theses of doctoral dissertation

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BACKGROUNDS AND OBJECTIVES

One of the most serious challenges in viticulture is the high susceptibility of grapevine to infections caused by various microorganisms—such as viruses, bacteria, and fungi—which can lead to significant economic losses in vineyards (PERAZZOLI et al. 2022). The health status of plants, including grapevine (*Vitis vinifera*), is influenced by a complex set of factors, encompassing site-specific conditions, climatic factors, agronomic practices (e.g. pruning systems, inter-row management, plant protection), as well as the structure of the surrounding natural and semi-natural vegetation (GRIGGS et al. 2021).

Beyond plant genotype, the composition of the plant-associated microbiome is strongly shaped by the surrounding vegetation, which not only influences the microclimate but also provides alternative host plants that may exert both negative and positive effects on one another. In addition, competition and cooperation among microbial communities, as well as vector-mediated dispersal, play an important role in shaping the dynamics of fungal communities (BULGARELLI et al. 2015; SAMAD et al. 2017; POITOU et al. 2017).

For these reasons, my doctoral research focuses on exploring the relationships among fungal communities inhabiting the leaves and woody tissues of grapevine and those of cultivated and native fruit-bearing plants occurring in its vicinity, including apricot (*Prunus armeniaca*), pear (*Pyrus communis*), dogrose (*Rosa canina*), and blackthorn (*Prunus spinosa*).

The primary objective of my research is to determine whether the organization and variability of these microbial communities are predominantly driven by abiotic factors (e.g. site conditions, seasonality, vintage effects) or by biotic influences (e.g. host plant, presence and spatial proximity of neighboring plants). Furthermore, I aim to assess whether co-occurring plant species may share economically important pathogens.

As grapevine is one of the most important cultivated crops in Hungary, a key focus of my research is the investigation of fungi causing Grapevine Trunk Diseases (GTDs) in other fruit-bearing plant species coexisting within the landscape mosaic. Previous studies have demonstrated that pathogens causing symptoms in grapevine—such as species belonging to the genera *Eutypa* and *Phaeoacremonium*—are also capable of inducing woody tissue damage in other host plants (MUNKVOLD 2001; DAMM et al. 2008; CLOETE et al. 2011; GUARNACCIA et al. 2022). This underscores the need for a landscape-scale, holistic approach that simultaneously considers the characteristics of microhabitats, interactions among host plant species, site conditions, seasonal dynamics, and interannual variability.

Through this integrative approach, the research aims to contribute novel insights into the understanding of fungal communities associated with the studied plant species. The expected results will enhance our understanding of the ecological functioning of fungi inhabiting woody tissues and leaves, as well as elucidate the interaction networks influencing the health of grapevine and surrounding plant species, thereby strengthening the ecological foundations of sustainable viticulture in the long term.

In summary, the objectives of my research are as follows:

1. To determine whether the development and structure of fungal communities are primarily influenced by abiotic factors (site conditions, seasonality, vintage effects) or by biotic factors (host plant species, presence and spatial proximity of neighboring plants).

2. To compare the fungal communities inhabiting the leaves and woody tissues of different host plants, including grapevine, apricot, pear, dogrose, and blackthorn.

3. To assess whether co-occurring plant species can share common, economically important pathogens.

4. To investigate the presence of pathogens associated with Grapevine Trunk Diseases (GTDs) in wild and cultivated fruit-bearing plant species occurring in the surroundings of vineyards.

5. To identify and compare the core mycobiome of each studied plant species and to distinguish stable, species-specific fungal components.

6. To apply indicator species analysis to identify fungi strongly associated with particular host plant species or sampling periods, thereby revealing the ecological processes shaping the organization of fungal communities.

MATERIALS AND METHODS

Sampling sites

Sampling was conducted in two vineyard sites of the Eger Wine Region: Kőlyuktető vineyard (47.863232° N, 20.385180° E; altitude 175 m a.s.l.) and Mihálynagytető vineyard (47.839640° N, 20.371429° E; altitude 224 m a.s.l.). The study areas are located on the outskirts of the city of Eger, on its southern side within the small-scale garden zone, where viticulture developed following medieval deforestation and has retained a mosaic-like spatial pattern to the present day (BARANYAI et al. 2017; KOVÁCS et al. 2019). In the immediate vicinity of the vineyards, forested, grassland, and residential patches occur, creating diverse ecological conditions that may influence the structure of microbial communities. While some areas are large and exclusively dedicated to viticulture, numerous smaller garden plots are also present, planted with grapevine or other cultivated crops. Consequently, sampling was carried out in well-managed vineyards and orchards embedded within a heterogeneous landscape mosaic, where cultivated areas alternate with early-successional, semi-natural habitats dominated by native shrubs such as dogrose (*Rosa canina*) and blackthorn (*Prunus spinosa*). Both fruit orchards and vineyards were managed under conventional plant protection practices.

Sampling and sampling strategy

Sampling was conducted on five plant species: grapevine, apricot, pear, dogrose, and blackthorn. These species occurred in close proximity within the two selected vineyard sites, forming a mosaic of cultivated plantations and semi-natural patches. This spatial arrangement made them suitable for investigating fungal community composition and the potential exchange and sharing of fungal pathogens among host plants. The selection of cultivated crops adjacent to grapevine (pear and apricot) was primarily based on the actual landscape composition of the sampling sites. However, according to the literature, several wood-inhabiting pathogens are shared between pear and grapevine (GUARNACCIA et al. 2022), making this comparison phytopathologically relevant. Apricot was included because an apricot orchard is present at the Mihálynagytető site and because, similarly to grapevine, apricot is highly affected by decline caused by wood-inhabiting diseases. Several studies have also demonstrated the presence of shared fungal pathogens between stone fruit trees—particularly apricot—and grapevine (DAMM et al. 2008). Whereas the selection of wild fruit-bearing shrubs (dogrose, blackthorn) was based on their frequent occurrence in ruderal habitats in Hungary.

The first sampling took place in March 2021 and was repeated in June and September, following the same schedule in the subsequent year. During the first sampling event, randomly selected plants were permanently marked, and samples were collected from the same individuals during subsequent samplings. For each plant, samples were collected from two distinct tissue types: leaves and woody tissues. Woody samples included bark, cambium, and sapwood and were obtained by excising a branch segment. In June and September, both leaf and woody tissue samples were collected, whereas in March, only woody tissues were sampled due to the absence of leaves. In total, 490 samples were collected from asymptomatic plants across the two sampling sites during the 2021 and 2022 growing seasons, including 196 leaf samples and 294 woody tissue samples. The woody tissue samples comprised 90 grapevine, 66 blackthorn, 60 dogrose, 42 pear, and 36 apricot samples, while the leaf samples included 60 grapevine, 44 blackthorn, 40 dogrose, 28 pear, and 24 apricot samples collected during the June and September sampling periods.

To assess the effect of distance from shrubland on fungal communities associated with grapevine, samples were collected from two vineyard rows. Grapevines located close to shrubland and those located further away were sampled. The vineyard selected for this analysis bordered a shrubland community on one side, while the remaining sides were adjacent to cultivated areas, including vineyards and pome fruit orchards. Sampling was conducted in March, June, and September. Grapevines close to the shrubland were located approximately 5 m from the shrubland edge, whereas the more distant vines were located approximately 80 m away.

DNA extraction, PCR and sequencing

Following field sampling, samples were immediately transported to the laboratory and stored at –80 °C. Subsequently, samples were freeze-dried under vacuum for 72 h to ensure complete dehydration and then pulverized using a steel-bead homogenizer (TissueLyser). Genomic DNA was extracted from approximately 20 mg of lyophilized and homogenized plant material per sample using a Plant DNA Isolation Kit (Macherey-Nagel GmbH & Co., Düren, Germany). DNA concentration and purity were measured with a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA).
The ITS2 region of the ribosomal DNA was amplified from all samples by PCR using the primers fITS7 (IHRMARK et al. 2012) and ITS4 (WHITE et al. 1990), to which Illumina overhang adapter sequences were attached (Illumina, San Diego, CA, USA). PCR reactions were performed in a total volume of 25 µL, containing 12.5 µL KAPA HiFi HotStart ReadyMix, 0.5 µM of each primer, 1 µL (~10 ng) of template DNA, and nuclease-free water.

Thermal cycling conditions consisted of an initial denaturation at 95 °C for 3 min, followed by 25–32 cycles of denaturation at 95 °C for 30 s, annealing at 56 °C for 30 s, and extension at 72 °C for 30 s, with a final elongation step at 72 °C for 5 min.
For sample identification, a second PCR was performed using the same primers supplemented with Illumina Nextera™ DNA CD Index sequences, following the Illumina dual-indexing strategy. PCR products were purified using AMPure XP magnetic beads (Beckman Coulter), quantified with the Qubit™ dsDNA HS Assay Kit (Thermo Fisher Scientific), and pooled in equimolar concentrations based on Qubit measurements. Library quality was assessed using an Agilent 2100 Bioanalyzer with the High Sensitivity DNA Kit. Sequencing was carried out on an Illumina MiSeq platform using the MiSeq Reagent Kit v2 (500 cycles), generating 250 bp paired-end reads. All molecular procedures—including PCR amplification, adapter ligation, library preparation, quality control, and sequencing—were performed by BIOMI Kft. (Gödöllő, Hungary) following Illumina's standard amplicon sequencing protocols.

Bioinformatic work

Raw sequence data were processed using the *dada2* package (CALLAHAN et al. 2016). Unlike OTU-based clustering approaches, this method reliably removes erroneous sequences while preserving fine-scale genetic variation, resulting in the generation of exact amplicon sequence variants (ASVs). This enables accurate characterization of intra- and interspecific fungal genetic diversity and allows for strain-level analyses. Based on visual inspection of sequence quality profiles, forward and reverse reads were truncated at 240 bp and 200 bp, respectively, to remove low-quality regions while retaining high-quality sequence data. Reads were then quality-filtered, paired-end reads were merged, chimeric sequences were removed, and ASVs were inferred using default settings.
Taxonomic assignment was performed using USEARCH v11 (EDGAR 2010) against the UNITE reference database (KÕLJALG et al. 2013), which contains dynamically defined fungal species hypotheses. Because sequence data from samples collected in 2021 were processed earlier, their initial taxonomic assignment was based on the UNITE version released on 25 July 2023. Following the processing of the 2022 dataset, both annual datasets were reprocessed using the UNITE version released on 19 February 2025 to ensure consistency and comparability. Taxonomic identification was accepted at a minimum sequence similarity threshold of 80%.

Functional guild assignment of fungal taxa was based on the curated and regularly updated FungalTraits database (PÕLME et al. 2020), with minor modifications. Non-litter- and non-wood saprotrophs (e.g. nectar or exudate

saprotrophs, sooty molds, soil saprotrophs, and undefined saprotrophs) were collectively classified as "saprotrophs." Additionally, non-pathogenic leaf-associated epiphytic and endophytic fungi were grouped under the category "leaf fungi" during the processing of the 2021 dataset.

Statistical analyses

Unless otherwise stated, all statistical analyses were performed in the R statistical environment. Samples containing fewer than 1,000 fungal sequences were excluded from further analyses. The community matrix was standardized using rarefaction-based normalization by randomly subsampling to the smallest library size with the *rrarefy* function of the *vegan* package (OKSANEN et al. 2007). All fungal ASV sequences analyzed in this study have been deposited in the GenBank database under accession numbers KIWX01000001–KIWX01004386 and KJJA00000000. In addition, two BioProjects were created (PRJNA1193836 and PRJNA1347291).

Because fungal community composition differed significantly ($p < 0.0001$) between leaf and woody tissues, communities associated with these two tissue types were analyzed separately when assessing the effects of hosts, seasons, and sites. The effects of categorical variables (e.g. host) on ASV richness and relative ASV abundance were examined using one-way and two-way analyses of variance (ANOVA). Only factors that showed significant effects in the one-way ANOVA were included in the two-way models. Pairwise differences were evaluated using Tukey's HSD post hoc test.

Differences in community composition among samples were visualized using non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarity matrices, with relative abundance data preprocessed using Hellinger transformation. NMDS ordinations were generated using the *metaMDS* function with 999 permutations. To test for differences among groups, permutational multivariate analysis of variance (PERMANOVA) was conducted using the *adonis* function with 9,999 permutations to estimate the proportion of variance explained by host plant species, sampling site, and sampling time. The effects of categorical variables were tested both individually and in combination, accounting for potential correlations among factors.

Overlap among ASVs associated with shared pathogens of the studied plant species, GTD-related pathogens, and the core mycobiome was visualized using Euler and Venn diagrams. Three-set diagrams were generated using the BioVenn web application (HULSEN et al. 2008). Because GTD pathogens primarily colonize the perennial woody tissues of grapevine and infect plants through pruning wounds or mechanical injuries (ROLSHAUSEN and KIYOMOTO 2012), analyses related to GTD pathogens were restricted to woody tissue samples. Fungal genera previously reported in the literature as

causal agents of Grapevine Trunk Diseases were treated as GTD-associated genera (GEIGER et al. 2022).

The core mycobiome was determined based on presence–absence data from samples collected from woody plant tissues. Taxa (ASVs) were considered members of the core mycobiome if they were present in at least 80% of all examined samples. This threshold allowed for the identification of stable, host-associated, and temporally persistent components of the microbial communities. The use of woody tissues was justified by their longevity and the previously reported temporal stability of their mycobiome compared to that of leaves, providing a more reliable basis for identifying persistent, plant-specific microbial components. Visualization of the core mycobiome using pie charts was performed with the *tidyverse*, *dplyr*, *reshape2*, *ggplot2*, and *RColorBrewer* packages.

Indicator species analysis was conducted using the *indicspecies* (DUFRÊNE and LEGENDRE 1997; DE CÁCERES et al. 2012) and *vegan* packages. The normalized dataset was transformed using Hellinger transformation with the *decostand()* function, and indicator species were identified using the *multipatt()* function with 999 permutations. Two grouping schemes were applied: (1) the five studied plant species constituted five distinct groups, and (2) for each plant species, the three sampling time points (March, June, and September) were treated as separate groups and compared with each other. This approach allowed for the disentanglement of host plant and temporal effects and the identification of specific indicator species associated with woody tissues.

RESULTS AND DISCUSSION

Fungal Richness and Abundance in Wood and Leaf Microhabitats

ASV richness and abundance of fungal communities associated with different host plant species showed marked differences between the investigated microhabitats (woody tissues and leaves). In woody samples, ASV richness differed significantly among host plants across all functional groups, with the exception of litter saprotrophs. In contrast, in leaf samples, a significant difference among host plants was observed in only one functional group, namely leaf fungi. Regarding abundance patterns, no significant differences among host plants were detected for any functional group in leaf samples, whereas in woody samples, significant differences were found among host plants for all functional groups except lichenized. Thus, our results indicate that significant differences in species richness among host plants were detectable exclusively in woody tissues. A study investigating leaf-associated fungal communities at the interface of vineyards and forest patches found no significant differences in fungal species richness between grapevine leaves and forest tree leaves during the summer months (FORT et al. 2016). This finding is consistent with our results, as we also detected no significant differences among the studied plant species in leaf samples collected in June and early September. Similarly, another study reported comparable diversity indices of leaf-associated fungi between forests and vineyards, while community composition differed between habitats. According to the authors, agricultural practices influence the structure rather than the diversity of fungal communities in vineyards (CASTAÑEDA et al. 2018). In contrast, abundance and species richness in woody tissues exhibited greater variability among host plant species. This pattern can be explained by the permanence of woody tissues and by the fact that bark represents a potentially important overwintering microhabitat for many fungal species (GROVE et al. 2004; CREGGER et al. 2018; GEIGER et al. 2022). A study on fungal communities associated with olive trees reported similar patterns, showing higher diversity values in leaves compared to flowers and fruits, regardless of season. Because olive trees are evergreen, leaves are present throughout the year and thus can support the establishment of a relatively stable fungal community (ABDELFATTAH et al. 2015). In deciduous trees and shrubs, however, this pattern is more pronounced in the contrast between woody tissues and leaves, as woody tissues do not undergo seasonal turnover and therefore provide a more temporally stable habitat for fungal communities.

Effects of Host, Site, and Season on Fungal Community Composition in Leaves and Wood

We examined the effects of host plant species, sampling site, and sampling time on the community composition of dominant functional groups, including plant pathogens, generalist saprotrophs, litter saprotrophs, and wood saprotrophs. PERMANOVA results indicated that all three factors—host plant , sampling site, and sampling time—had a significant effect on fungal community composition, both when considering the entire fungal assemblage and when analyzing each dominant functional group separately. In the leaves, sampling date, which occurred in two different seasons (summer and autumn), had the largest effect on fungal composition variation, explaining 16.3% of the variance. Of the three factors, host plant was the second most influential (R^2 = 10.3%, p = 0.0001), and although less influential, site was still a significant factor (R^2 = 7%, p = 0.0001). This pattern was also evident for plant pathogens. This is because, again, sampling time was by far the most determinant factor, explaining 26% of the variance. This was followed by host plant (R^2 = 7.6%, p = 0.0174) and then sampling site (R^2 = 4.5%, p = 0.0017). In contrast, for saprotrophs, the host plant was the dominant factor, explaining 9.8% of the compositional variance. Sampling time was the least influential factor (R^2 = 4.7%, p = 0.0001), and site was the second most influential (R^2 = 6.3%, p = 0.0001). This trend changed again for the litter saprotrophs, where, after host plant (R^2 = 12.4%, p = 0.0001), sampling time (R^2 = 8.4%, p = 0.0001) was the most influential factor, followed by site (R^2 = 6.5%, p = 0.0001).

In woody parts, the host effect was the most influential on fungal community composition (R^2 = 15.7%, p = 0.0001), followed by the sampling site (R^2 = 5.1%, p = 0.0001) and sampling time (R^2 = 4.8%, p = 0.0001) (Figure 4). The composition of the phytopathogenic fungal communities from woody parts was also strongly influenced by the identity of the host plants, which explained 13.6% of the compositional variance, but in this case, sampling site and sampling date were almost equally important, explaining 5.4% of the compositional variance for sampling area and 5.5% for sampling date. The composition of saprotrophs was most strongly determined by the host plant in the wood samples (R^2 = 12.4%, p = 0.0001). This was followed by the sampling time (R^2 = 7.7%, p = 0.0001) rather than the area, as was the case for leaves. For wood saprotrophs, host plant (R^2 = 11.8%, p = 0.0001) was also the determinant of fungal community composition, followed by sampling time (R^2 = 5.6%, p = 0.0001) and finally site (R^2 = 2.7%, p = 0.0003).

According to the PERMANOVA analysis, the host plant was the most dominant factor shaping the fungal communities of woody tissues. The significant effect of host plant species on the wood-associated microbiome was also demonstrated by Krah et al. (2018), who showed that host species identity is more determinant for fungal communities in wood than environmental factors. Although host plant species also had a significant effect on leaf-

associated fungal communities, seasonality proved to be the primary driving factor in this case. The sampling site contributed significantly to the variance of fungal communities in both leaf and woody samples; however, its influence was less pronounced compared to the other two variables.

In the case of leaves, our results do not fully align with other studies that investigated the composition and dynamics of leaf-associated fungal communities across multiple habitats and sampling periods. These studies suggest that host plant identity and tissue niche are more important determinants of community structure than seasonality. Although seasonality exerts a significant effect on microbial communities, the differences between seasons are smaller than those observed between host plant species. Moreover, the interaction between season and host plant explains less variance than host plant identity alone (LI et al. 2022; HE 2023). For plant pathogenic fungal communities, seasonality had a stronger effect in leaves than in woody tissues, a pattern supported by several studies. These investigations highlight that phytopathogenic leaf fungal communities exhibit seasonal successional patterns, as newly formed leaves are colonized in each growing season. This phenomenon is particularly pronounced in deciduous species, where fungi recolonize leaves every spring (TANUNCHAI et al. 2022; VANWALLENDAEL et al. 2022). In contrast, seasonal changes are less influential in woody tissues due to their structural stability.

These results emphasize that while fungal communities in leaves are dynamic and seasonally variable, more stable communities are found in woody tissues. The differences between leaf and woody tissues can also be attributed to niche-based processes, as many fungal species specialize in specific plant tissue types (MARTÍNEZ-DIZ et al. 2019; MOLNÁR et al. 2022; GEIGER et al. 2022).

The vineyard site— a component of terroir—plays a significant role in shaping grapevine-associated fungal communities (GEIGER et al. 2022; LEAL et al. 2024). The results of the present study revealed significant differences in fungal community composition between the two sampling sites (Kőlyuktető and Mihálynagytető vineyards). Given that the two sites are geographically close and experience similar climatic conditions, the observed differences are unlikely to be of climatic origin. Instead, they are more likely attributable to differences in soil type, topography, vegetation composition, and vineyard management practices. This interpretation is supported by previous studies demonstrating that fungal community structure is strongly influenced by microclimatic factors, soil properties, vegetation density and diversity, environmental stressors (e.g., pollution and anthropogenic disturbance), and plant protection practices (CASTAÑEDA et al. 2018; LIU et al. 2023; LEPINAY et al. 2024).

Effect of Shrub Proximity on Grapevine Fungal Communities

The effect of shrubland proximity (near: 5 m, far: 80 m) was tested by comparing the fungal communities of grapevines located close to and farther from the shrubland. When comparing near and far grapevines separately, no statistically significant differences were found in either the leaves or the woody tissues. According to the PERMANOVA test, distance from the shrubland explained 9.2% of the variation in leaf-associated fungal communities (p = 0.858) and 8.1% of the variation in wood-associated communities (p = 0.5085). These results indicate that, at the spatial scale investigated, proximity to shrubland was not a significant factor shaping the composition of fungal communities. In contrast, the NMDS analysis revealed that fungal communities in woody tissues differed significantly between the shrub and the grapevines (PERMANOVA: R^2 = 24.2%, p = 0.0004). However, the communities of grapevines located closer to or farther from the shrub were similar to each other, suggesting that distance from the shrub did not substantially influence community structure. The observed difference is therefore primarily attributable to the host plant species: the composition of fungal communities in woody tissues was determined more by the plant species itself than by the grapevines' position relative to the shrub. The fungal community composition of leaves did not differ significantly between the shrub and the grapevines (PERMANOVA: R^2 = 18.6%, p = 0.5155). The lack of significant separation indicates that, in contrast to woody tissues, neither the host plant species nor the distance from the shrub strongly influenced the structure of foliar fungal communities. Thus, fungal communities in leaves appear to be more homogeneous across host plant types and positions relative to the shrub. In the case of leaves, we examined the entire leaf-associated community, including both endophytic and epiphytic fungi. Accordingly, leaf-associated communities did not show significant differences between shrubs and grapevines, whereas a clear separation was observed in woody tissues. This indicates that host plant species is the primary factor shaping the structure of fungal communities, with distinct patterns across tissue types: fungal communities inhabiting woody tissues are strongly host-species specific, while leaf-associated communities are more homogeneous, partly due to the dispersal of epiphytic fungi. This is consistent with our previous analyses, which confirmed that the host plant strongly shapes fungal communities in woody tissues, whereas its influence is less dominant in leaves.

Shared plant pathogenic fungi among the studied plant species

The highest number of plant pathogenic fungal ASVs was detected in dogrose samples (both woody tissues and leaves; 1,015 ASVs), followed by blackthorn with 691 ASVs, grapevine with 631 ASVs, and pear with 519 ASVs. Apricot samples contained the lowest number of plant pathogenic fungal ASVs (488

ASVs). Across all studied plant species, a total of 264 plant pathogenic fungal ASVs were shared, which were identified at the genus level. The most dominant genera among these shared ASVs were *Alternaria*, *Phyllosticta*, *Taphrina*, *Pseudopezicula*, *Seimatosporium*, and *Phaeomoniella*. Subsequently, we examined the overlap of plant pathogenic fungal ASVs between cultivated fruit crops and grapevine, as well as between native fruit-bearing plants and grapevine. The complete overlap among grapevine, pear, and apricot comprised 284 plant pathogenic fungal ASVs. Genus-level identification revealed that *Alternaria* was again the most dominant genus, followed by *Phyllosticta*. Additional characteristic genera included *Taphrina*, *Pseudopezicula*, *Seimatosporium*, and *Phaeomoniella*. Grapevine, blackthorn, and dogrose shared 461 plant pathogenic fungal ASVs. Among these, *Alternaria* and *Phyllosticta* were again the most ASV-rich genera, while *Diaporthe* and *Didymella* were also present at high relative abundances. The extensive overlap of phytopathogenic fungi among the studied plant species suggests that these plants may act as microbial reservoirs for plant pathogenic fungi. This role is critical in the dynamics of plant diseases, as the majority of the detected phytopathogens are capable of persisting in asymptomatic host plants and likely constitute part of the natural microbiome of the examined crop species. Among the shared phytopathogenic fungi, members of the genus *Alternaria* were detected at the highest frequency. This is consistent with the ecology of *Alternaria* species, which are among the most widespread and significant endophytic and opportunistic phytopathogenic fungi, but may also occur as saprotrophs. As pathogens, *Alternaria* species are known to cause storage diseases and secondary infections in a wide range of agricultural crops (SIMMONS 2007; LAWRENCE et al. 2016; SINGH et al. 2016).

Presence of Grapevine Trunk Disease–associated pathogens in the studied plant species

A total of 85 ASVs representing Grapevine Trunk Disease (GTD)–associated pathogens were identified in the cultivated plant species. Among these, 12 ASVs were shared by grapevine, apricot, and pear, representing 14% of all detected GTD-related ASVs. Pairwise comparisons among host plants revealed the highest overlap between pear and grapevine (23.5%), followed by grapevine and apricot (9.4%), and finally apricot and pear (2.4%). Genus-level identification indicated that the following genera were shared among grapevine, pear, and apricot: *Diaporthe*, *Eutypa*, *Phaeomoniella*, *Phaeoacremonium*, and *Neofusicoccum*.

Comparisons between grapevine and native shrub species yielded similarly noteworthy results. A total of 79 ASVs representing GTD-associated pathogens were detected across the three studied plant species, of which 23 ASVs were shared (29% overlap). In pairwise comparisons, the highest overlap was observed between grapevine and dogrose (16.5%), followed by

grapevine and blackthorn (14%), and finally blackthorn and dogrose (6.3%). Genus-level identification revealed the following shared genera among grapevine, dogrose, and blackthorn: *Diaporthe*, *Phaeomoniella*, *Neofusicoccum*, and *Truncatella*.

Our results demonstrate that GTD-associated pathogens are present in all examined plant species, albeit at different relative abundances, indicating varying levels of host susceptibility. The substantial overlap of GTD-associated fungal taxa detected in the woody tissues of different host plants suggests that all examined species may serve as potential hosts for fungi responsible for grapevine trunk diseases. Consequently, these plants may also function as potential inoculum sources for nearby vineyards.

Overall, our findings indicate that GTD-associated pathogens are able to persist and infect the examined plant species and may spread from these hosts into adjacent vineyards. Therefore, disease management strategies should not be restricted to the vineyard scale alone. It is important to note that most GTD-associated pathogens are commonly present in grapevine, often without visible symptoms. These fungi are generally considered opportunistic pathogens that become active under environmental or management-related stress conditions affecting the host plant (GEIGER et al. 2022; LEAL et al. 2024). Consequently, improving cultivation practices—not only to enhance yield and quality but also to strengthen plant resilience—is crucial for mitigating the impacts of Grapevine Trunk Diseases.

Identification and comparison of the core mycobiome of the studied plant species

The results showed that both the richness and the composition of the core mycobiome differed substantially among the investigated host plant species. Dogrose (52 ASVs) and blackthorn (98 ASVs) harbored relatively rich core communities, whereas among the cultivated species, grapevine (35 ASVs) and especially pear (29 ASVs) contained considerably fewer core taxa. This pattern can be partly explained by the different ecological contexts of cultivated versus wild host plants, which may influence both the composition and stability of microbial communities. In contrast to the other cultivated species, apricot contained a markedly higher number of core fungal taxa (81 ASVs) and thus represented an exception.

One possible explanation is the shared taxonomic affiliation of apricot and blackthorn, as both belong to the genus *Prunus*, which may contribute to the more diverse core fungal community observed in apricot. However, it is important to emphasize that robust support for this inference would require additional studies including further *Prunus* species (both cultivated and wild; e.g. plum, sweet cherry, peach, wild cherry, cherry plum), in order to evaluate how broadly a potential "*Prunus* effect" on core mycobiome richness can be generalized.

Dogrose and blackthorn occur in semi-natural habitats and are exposed to diverse microbial sources (soil, insects, animals, neighboring plants), which can promote both diversity and stability of their associated communities. In parallel, the genetic background of wild plants —through phenotypic and physiological traits adapted to local environmental conditions — may indirectly shape microbiome composition, potentially providing adaptive advantages and leading to community structuring by natural selection (BARNES et al. 2025). In contrast, intensively managed cultivated species such as grapevine and pear are regularly subjected to plant protection interventions, often occur in (near-) monocultures (particularly grapevine), and may have developed narrower microbial associations during domestication (SOLDAN et al. 2021). Soldan et al. (2021) examined how domestication altered plant capacity to shape and regulate the microbiome and introduced the "double-leash" model, in which human selection acts on the plant while the plant, in turn, regulates its associated microorganisms. Domestication-driven phenotypic changes—such as seed size, metabolite composition, or tissue traits—can strongly influence the plant's ability to select and maintain its microbiome. Combined effects of agronomic practices and genetic change (e.g. monoculture, genetically homogeneous plantations, intensive pesticide use) often result in a narrower and less diverse core microbiome in cultivated species compared to their wild relatives. The study further suggests that deliberate microbiome management—such as restoring wild-type associations—may improve crop health and resilience, because traits directly selected during breeding are not necessarily linked to higher overall fitness. It is also plausible that stronger immune responses and higher filtering capacity in cultivated species contribute to fewer taxa meeting the stringent criteria of the core definition (AQUEEL et al. 2024). In a study comparing the core microbiome of two cotton species—one susceptible to cotton leaf curl disease (CLCuD; *Gossypium hirsutum*) and one resistant (*Gossypium arboreum*)—under viral infection, the resistant species exhibited substantially higher microbial diversity. Their results indicated an inverse relationship between core microbiome diversity and disease susceptibility, providing a potential basis for developing biocontrol agents and improving pathogen resistance in plants (AQUEEL et al. 2024).

A further potential explanation for the high core diversity observed in apricot is plantation age. In contrast to the sampled grapevine vineyards (established in 1993) and the pear orchard (established in 2016), which consisted of mature, well-established plants, the apricot orchard was only 3–4 years old at the time of sampling (established in 2018). Thus, these young trees may not yet have developed a strongly selective, stable microbial community. We assume that the young orchard represents a more "open" ecological system, allowing microorganisms from multiple sources to persist over longer periods. Moreover, at early developmental stages, selective pressures imposed by pathogens and plant protection practices may not yet be strong enough to cause

a marked narrowing of the core community; therefore, the rich core community observed in apricot likely reflects a transitional state. In *Populus tomentosa*, for example, the root microbiome of young trees was shown to be richer and more diverse but less stable, whereas older trees had narrower communities that were more strongly host-regulated and more stable (XIE et al. 2023). This supports the notion that the rich core community observed in young apricot orchards may gradually narrow as trees age.

When comparing the core mycobiomes of the five host plants, we identified 13 shared ASVs in total, including five fungal taxa that were detectable in all plant species and at all sampling time points: *Aureobasidium intercalariosporum*, *Buckleyzyma aurantiaca*, *Filobasidium wieringae*, *Rinodina pyrina*, and *Xenodidymella clematidis*. In addition, it is important to note that *Alternaria brassicae* was a shared core member across all examined hosts except grapevine, where its stable occurrence did not reach the 80% prevalence threshold.

The shared core taxa represent multiple ecological strategies, suggesting that the stability of the plant mycobiome may be maintained by the co-occurrence of fungi with different life histories. *Aureobasidium intercalariosporum* and *Filobasidium wieringae* are typical generalists—broad host-range epiphytes and endophytes—with documented biocontrol potential (GLUSHAKOVA and KACHALKIN 2017; WU et al. 2023; ABO-ELYOUSR et al. 2024; RENSINK et al. 2024). *Rinodina pyrina* is a lichen-forming fungus that likely colonizes plants continuously from the surrounding environment and thus persists as a stable background component (VARGAS et al. 2013). *Xenodidymella clematidis* occurs primarily as an endophyte but is also known as an opportunistic pathogen, indicating that it may play a pathogenic role despite asymptomatic presence (KARIMI et al. 2024). Their joint occurrence suggests that, within the shared microbial core of cultivated and wild plants, multiple ecological functions collectively contribute to the stability of plant–microbe interactions.

Indicator species in the studied plant species

Applying indicator species analysis across five co-occurring host plants is methodologically justified because the shared environmental background provides controlled conditions for detecting host effects. Consequently, indicator taxa identified in this framework are more likely to be associated with host traits rather than with differences in habitat conditions.
Substantial differences were found among the five host plants in the number of indicator ASVs: 305 ASVs were identified from blackthorn, 83 from dogrose, 103 from apricot, 332 from pear, and 333 from grapevine. Thus, blackthorn harbored many more indicator taxa than, for example, dogrose.

Across indicator communities, the most frequently assigned functional groups were plant pathogens (223 ASVs) and diverse saprotrophic fungi (258 ASVs). In addition, mycoparasites and epiphytes were present in all hosts, although at lower proportions. Altogether, these results suggest that each host plant is associated with a characteristic microbial community that also differs functionally.

Indicator species analysis further revealed that many fungi were exclusively associated with a single host plant, indicating specialization in host–microbe relationships. This is particularly important for pathogenic taxa, as they may represent host-specific disease agents.

The proportional distribution of functional categories among indicator taxa differed markedly among host plants. In dogrose, plant pathogens dominated the indicator community, accounting for more than 60% of ASVs, whereas other functional groups were scarcely represented. In contrast, grapevine and pear communities showed a more balanced structure, where—besides pathogens—wood-decaying saprotrophs and generalist saprotrophs also represented substantial proportions. In blackthorn, mycoparasites (14.7%) and leaf-associated endophytes (8.1%) were present at comparatively high proportions, whereas in apricot, nearly one-third of the community belonged to the plant pathogen functional group.

Overall, our results demonstrate that host-associated fungal communities differ not only in diversity but also in functional composition. Species-specific occurrence of pathogens may indicate differences in disease risk, while the presence of saprotrophs and endophytic fungi highlights the broad ecological functionality of host-associated microbial communities. Comparing co-occurring plants makes it clear that each host species possesses a distinct, functionally differentiated microbial profile, consistent with other studies showing that host plant identity strongly shapes the composition of pathogenic, saprotrophic, and mycorrhizal fungal communities even at close spatial proximity (LIANG et al. 2023).

CONCLUSIONS AND RECOMMENDATIONS

The results of this research provide new insights into the relationships among fungal communities associated with grapevine and with surrounding cultivated and native fruit-bearing plant species. Based on investigations conducted over two growing seasons in two vineyard sites of the Eger Wine Region, it can be concluded that the organization of microbial communities is jointly shaped by host plant identity, plant organ type, seasonality, and site-specific conditions. The dynamics and diversity of fungal communities are influenced not only by environmental factors, but also by the biological and ecological characteristics of plant species, as well as by cultivation practices.

Fungal communities inhabiting woody tissues and leaves were clearly separated from each other in both composition and structure. In woody tissues, fungal community structure differed significantly among host plant species, with host identity emerging as the strongest determining factor. Woody tissues provide a permanent and protected microhabitat in which microbial communities are more stable and less responsive to short-term environmental fluctuations. In contrast, fungal communities inhabiting leaves exhibited pronounced seasonal dynamics: seasonal variation played a much greater role in shaping these communities than host plant species or site conditions. This suggests that leaf-associated microorganisms form short-lived, rapidly responding, and dynamically changing communities, whereas fungi inhabiting woody tissues persist as long-term stabilized, host-dependent communities.

Significant differences in fungal community composition were detected between the two sampling sites (Kőlyuktető and Mihálynagytető), likely reflecting differences in microclimatic conditions and soil characteristics. These findings emphasize that fungal community structure is shaped by fine-scale, local factors that can be integrated into the concept of terroir; thus, microbial communities may be interpreted as ecological imprints of vineyard-specific environmental conditions.

According to the results, the proximity of shrub vegetation did not significantly influence grapevine-associated fungal communities in either leaves or woody tissues at the examined spatial scale (5–80 m). This may indicate that such spatial distances are insufficient to detect dispersal gradients. However, the findings further reinforce the dominant role of host plant identity in structuring fungal communities, as significant differences were driven primarily by differences among host species rather than by their spatial arrangement.

One of the most important findings of this study is the substantial overlap observed among phytopathogenic fungal communities associated with different plant species. Phytopathogenic genera such as *Alternaria*, *Phyllosticta*, *Taphrina*, *Phaeomoniella*, and *Diaporthe* occurred across multiple host plants, confirming that co-occurring species may function as microbial reservoirs for fungal pathogens. Pathogens associated with

grapevine trunk diseases—such as members of the genera *Phaeomoniella*, *Neofusicoccum*, and *Diaporthe*—were detected in all examined plant species. This finding confirms the potential role of surrounding fruit trees and reveals, in the case of shrubs, that these *Rosaceae* species may act as inoculum sources for vineyards. This recognition necessitates a fundamentally new perspective in grapevine health management, as pathogen spread cannot be interpreted solely at the vineyard scale, but must be examined at the landscape scale in relation to neighboring vegetation. Moreover, because asymptomatic grapevine plants were sampled in this study, the results suggest that GTD-associated pathogens may constitute a natural component of the woody plant microbiome. Consequently, GTD management should primarily focus on maintaining good plant vitality, which may play a key role in preventing disease development.

Analysis of the shared core mycobiome revealed that the studied plant species partly share stable fungal components across hosts. *Aureobasidium intercalariosporum*, *Buckleyzyma aurantiaca*, *Filobasidium wieringae*, *Rinodina pyrina*, and *Xenodidymella clematidis* were detected in all host plants, suggesting that these generalist species function as ecological stabilizers. At the same time, several host-specific core taxa were identified, indicating host-driven ecological filtering. Domesticated, intensively managed crop species such as grapevine and pear exhibited narrower core communities, whereas the wild dogrose and blackthorn harbored richer core mycobiomes. This difference likely arises from the combined effects of cultivation practices, plant protection interventions, and host adaptive mechanisms, reinforcing the notion that intensive agricultural management may lead to reduced microbial diversity.

Indicator species analysis demonstrated that host plants co-occurring under identical environmental conditions are associated with distinct fungal communities that also differ functionally. The presence of host-specific indicator taxa indicates specialization in plant–microbe interactions and the potential occurrence of host-specific pathogens. Seasonal patterns further highlight that microbial communities change dynamically over time, influencing infection pressure and plant health. Based on these findings, long-term monitoring and functional investigation of host plant–microbe interactions are recommended to improve pathogen forecasting and to develop targeted plant protection strategies.

Overall, the microbial interaction network among grapevine and surrounding plant species is complex, multi-layered, and temporally dynamic. Fungal community composition is simultaneously shaped by host plant biology, structural and chemical differences among tissues, abiotic environmental factors, and human intervention. The results indicate that maintaining microbial diversity and suppressing pathogens cannot be decoupled from landscape structure and the presence of natural vegetation. Biodiversity

conservation and plant health management therefore need to be addressed in an integrated ecological framework.

In conclusion, this research contributes to a deeper ecological understanding of fungal communities associated with grapevine and neighboring plant species and establishes a new foundation for the development of sustainable viticulture. The identified patterns demonstrate that grapevine health and resilience are closely linked to the microbial networks of surrounding vegetation. Future plant health research and practice should consider the landscape-scale distribution and interactions of microorganisms to develop more effective and ecologically balanced systems. Detailed mapping and functional characterization of fungal communities provide opportunities to maintain natural biological balance, thereby supporting the ecological foundations of sustainable and environmentally conscious grapevine and fruit production.

Future research should focus on long-term, multi-year investigations of host plant–microbe interactions and on elucidating the functional roles of fungal communities using metagenomic and metabolomic approaches. Analysis of microbial network dynamics in relation to land use, plant protection practices, and climatic factors is warranted to improve understanding of the ecological background of plant health. Such integrated approaches may contribute to the development of sustainable and ecologically balanced grapevine and fruit production systems.

NEW SCIENTIFIC RESULTS

1. This study is the first to apply a landscape-scale, multi-host DNA metabarcoding approach to investigate fungal communities associated with grapevine and co-occurring cultivated and wild fruit-bearing plant species.

2. Within the same individual plant, mycobiome composition differs markedly among plant tissues and is shaped by distinct abiotic and biotic factors; host plant identity is the primary driver of fungal community assembly in woody tissues, whereas seasonal variation predominates in leaves.

3. A substantial overlap was detected among phytopathogenic fungal communities associated with grapevine and with surrounding cultivated and native fruit-bearing plant species.

4. This study is the first to describe dogrose and blackthorn as potential natural host plants for multiple fungal genera associated with Grapevine Trunk Diseases (GTDs).

5. The core mycobiome of woody tissues in apricot, pear, blackthorn, and dogrose was identified for the first time, and shared core members among the studied plant species were also determined for the first time within a habitat mosaic.

6. This research is the first to compare fungal communities of grapevine and neighboring cultivated and wild fruit-bearing plant species using indicator species analysis.

REFERENCES

1. ABDELFATTAH, A., LI DESTRI NICOSIA, M. G., CACCIOLA, S. O., DROBY, S., SCHENA, L. (2015) Metabarcoding analysis of fungal diversity in the phyllosphere and carposphere of olive (*Olea europaea*). *PLoS One*, 10: e0131069. DOI: 10.1371/journal.pone.0131069.
2. ABO-ELYOUSR, K. A. M., IMRAN, M., SALLAM, N. M. A., ABDEL-AAL, A. M. K., ASSIRI, M. E., ABDEL-RAHIM, I. R. (2024) Sustainable biocontrol of purple blotch disease in *Allium cepa* L. by biocontrol yeasts, *Pichia kluyveri* and *Filobasidium wieringae*. *Egyptian Journal of Biological Pest Control*, 34(1): 11. DOI: 10.1186/s41938-024-00776-6.
3. AQUEEL, R., BADAR, A., ROY, N., IJAZ, U. Z., MALIK, K. A. (2024) Disease resistance correlates with core microbiome diversity in cotton. Current Microbiology, 81(9): 302. DOI: 10.1007/s00284-024-03827-1.
4. BARANYAI, G., BALOGH, A., NÉMETH, S., POZSGAI, A. (2017) Vas megye elfeledett „hegyei". Történeti Földrajzi Közlemények, 5(3–4): 205–216.
5. BARNES, C. J., BAHRAM, M., NICOLAISEN, M., GILBERT, M. T. P., VESTERGÅRD, M. (2025) Microbiome selection and evolution within wild and domesticated plants. Trends in Microbiology, 33(4): 447–458.
6. BULGARELLI, D., GARRIDO-OTER, R., MÜNCH, P. C., WEIMAN, A., DRÖGE, J., PAN, Y., MCHARDY, A. C., SCHULZE-LEFERT, P. (2015) Structure and function of the bacterial root microbiota in wild and domesticated barley. Cell Host & Microbe, 17(3): 392–403. DOI: 10.1016/j.chom.2015.01.011.
7. CALLAHAN, B. J., MCMURDIE, P. J., ROSEN, M. J., HAN, A. W., JOHNSON, A. J. A., HOLMES, S. P. (2016) DADA2: high-resolution sample inference from Illumina amplicon data. Nature Methods, 13(7): 581–583. DOI: 10.1038/nmeth.3869.
8. CASTAÑEDA, L. E., MIURA, T., SÁNCHEZ, R., BARBOSA, O. (2018) Effects of agricultural management on phyllosphere fungal diversity in vineyards and the association with adjacent native forests. PeerJ, 6: e5715. DOI: 10.7717/peerj.5715.
9. CLOETE, M., FOURIE, P. H., DAMM, U., CROUS, P. W., MOSTERT, L. (2011) Fungi associated with die-back symptoms of apple and pear trees, a possible inoculum source of grapevine trunk disease pathogens. *Phytopathologia Mediterranea*, 50: S176–S190.
10. CREGGER, M. A., VEACH, A. M., YANG, Z. K., CROUCH, M. J., VILGALYS, R., TUSKAN, G. A., et al. (2018) The *Populus* holobiont:

dissecting the effects of plant niches and genotype on the microbiome. *Microbiome*, 6: 31. DOI: 10.1186/s40168-018-0413-8.
11. DAMM, U., MOSTERT, L., CROUS, P. W., FOURIE, P. H. (2008) Novel *Phaeoacremonium* species associated with necrotic wood of *Prunus* trees. *Persoonia – Molecular Phylogeny and Evolution of Fungi*, 20(1): 87–102. DOI: 10.3767/003158508X324227.
12. DE CÁCERES, M., LEGENDRE, P., WISER, S. K., BROTONS, L. (2012) Using species combinations in indicator value analyses. *Methods in Ecology and Evolution*, 3: 973–982. DOI: 10.1111/j.2041-210X.2012.00246.x. DOI: 10.3389/fpls.2022.1069886.
13. DUFRÊNE, M., LEGENDRE, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67(3): 345–366. DOI: 10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2.
14. EDGAR, R. C. (2010) Search and clustering orders of magnitude faster than BLAST. *Bioinformatics*, 26(19): 2460–2461. DOI: 10.1093/bioinformatics/btq461.
15. FORT, T., ROBIN, C., CAPDEVIELLE, X., DELIÈRE, L., VACHER, C. (2016) Foliar fungal communities strongly differ between habitat patches in a landscape mosaic. *PeerJ*, 4: e2656. DOI: 10.7717/peerj.2656.
16. GEIGER, A., KARÁCSONY, Z., GOLEN, R., VÁCZY, K. Z., GEML, J. (2022) The compositional turnover of grapevine-associated plant pathogenic fungal communities is greater among intraindividual microhabitats and terroirs than among healthy and esca-diseased plants. *Phytopathology*, 112(5): 1029–1035. DOI: 10.1094/PHYTO-05-21-0190-R.
17. GLUSHAKOVA, A. M., KACHALKIN, A. V. (2017) Endophytic yeasts in *Malus domestica* and *Pyrus communis* fruits under anthropogenic impact. *Microbiology*, 86(1): 128–135. DOI: 10.1134/S0026261716060102.
18. GRIGGS, R. G., STEENWERTH, K. L., MILLS, D. A., CANTU, D., BOKULICH, N. A. (2021) Sources and assembly of microbial communities in vineyards as a functional component of winegrowing. *Frontiers in Microbiology*, 12: 673810. DOI: 10.3389/fmicb.2021.673810.
19. GROVE, G. G. (2004) Perennation of *Uncinula necator* in vineyards of eastern Washington. *Plant Disease*, 88: 242–247. DOI: 10.1094/PDIS.2004.88.3.242.
20. GUARNACCIA, V., KRAUS, C., MARKAKIS, E., ALVES, A., ARMENGOL, J., EICHMEIER, A., COMPANT, S., GRAMAJE, D. (2022) Fungal trunk diseases of fruit trees in Europe: pathogens, spread and future directions. *Phytopathologia Mediterranea*, 61(3): 563–599. DOI: 10.36253/phyto-14167.

21. HE, C., MENG, D., LI, W., LI, X., HE, X. (2023) Dynamics of endophytic fungal communities associated with cultivated medicinal plants in a farmland ecosystem. *Journal of Fungi*, 9: 1165.
22. HULSEN, T., DE VLIEG, J., ALKEMA, W. (2008) BioVenn – a web application for the comparison and visualization of biological lists using area-proportional Venn diagrams. *BMC Genomics*, 9: 488. DOI: 10.1186/1471-2164-9-488.
23. IHRMARK, K., BÖDEKER, I. T., CRUZ-MARTINEZ, K., FRIBERG, H., KUBARTOVA, A., SCHENCK, J., STRID, Y., et al. (2012) New primers to amplify the fungal ITS2 region – evaluation by 454-sequencing of artificial and natural communities. FEMS Microbiology Ecology, 82(3): 666–677.
24. KARIMI, M., MEHRABI-KOUSHKI, M., FAROKHINEJAD, R., BEIGI, S. (2024) Additional new species of Xenodidymella from pasture-medicinal plants in Iran. Antonie van Leeuwenhoek, 117(1): 110. DOI: 10.1007/s10482-024-02007-2.
25. KÕLJALG, U., NILSSON, R. H., ABARENKOV, K., TEDERSOO, L., TAYLOR, A. F., BAHRAM, M., et al. (2013) Towards a united paradigm for sequence-based identification of fungi. Molecular Ecology, 22: 5271–5277. DOI: 10.1111/mec.12481.
26. KOVÁCS, G., LENNER, T., CSAPÓ, T. (2019) Eger történeti földrajza és településmorfológiája. Településföldrajzi Tanulmányok, 8(2).
27. KRAH, F. S., SEIBOLD, S., BRANDL, R., BALDRIAN, P., MÜLLER, J., BÄSSLER, C. (2018) Independent effects of host and environment on the diversity of wood-inhabiting fungi. Journal of Ecology, 106: 1428–1442. DOI: 10.1111/1365-2745.12946.
28. LAWRENCE, D. P., ROTONDO, F., GANNIBAL, P. B. (2016) Biodiversity and taxonomy of the pleomorphic genus Alternaria. Mycological Progress, 15(1): 1–22. DOI: 10.1007/s11557-015-1144-x.
29. LEAL, C. M., GEIGER, A., MOLNÁR, A., VÁCZY, K. Z., KGOBE, G., ZSÓFI, Z., GEML, J. (2024) Disentangling the effects of terroir, season, and vintage on the grapevine fungal pathobiome. Frontiers in Microbiology, 14. DOI: 10.3389/fmicb.2023.1322559.
30. LEPINAY, C., VĚTROVSKÝ, T., CHYTRÝ, M., et al. (2024) Effect of plant communities on bacterial and fungal communities in a Central European grassland. *Environmental Microbiome*, 19: 42. DOI: 10.1186/s40793-024-00583-4.
31. LI, M., HONG, L., YE, W., WANG, Z., SHEN, H. (2022) Phyllosphere bacterial and fungal communities vary with host species identity, plant traits and seasonality in a subtropical forest. *Environmental Microbiome*, 17(1): 29. DOI: 10.1186/s40793-022-00423-3.
32. LIANG, S., ARRAIANO-CASTILHO, R., NEUENKAMP, L., LI, H., BAI, Z., ZHANG, M., YIN, J., YUAN, Z., WANG, X. (2023)

Rhizosphere fungal community assembly varied across functional guilds in a temperate forest. *Ecological Processes*, 12(1): 6. DOI: 10.1186/s13717-023-00417-0.
33. LIU, S., XIONG, C., LIN, L., KEYHANI, N. O., ZHU, M., ZHAO, Z., et al. (2023) Assessing the structure and diversity of fungal community in plant soil under different climatic and vegetation conditions. *Frontiers in Microbiology*, 14: 1288066. DOI: 10.3389/fmicb.2023.1288066.
34. MARTÍNEZ-DIZ, M. D. P., ANDRÉS-SODUPE, M., BUJANDA, R., DÍAZ-LOSADA, E., EICHMEIER, A., GRAMAJE, D. (2019) Soil–plant compartments affect fungal microbiome diversity and composition in grapevine. *Fungal Ecology*, 41: 234–244. DOI: 10.1016/j.funeco.2019.07.003.
35. MOLNÁR, A., GEML, J., GEIGER, A., LEAL, C. M., KGOBE, G., TÓTH, A. M., VILLANGÓ, S., et al. (2022) Exploring relationships among grapevine chemical and physiological parameters and leaf and berry mycobiome composition. *Plants*, 11(15): 1924. DOI: 10.3390/plants11151924.
36. MUNKVOLD, G. P. (2001) Eutypa dieback of grapevine and apricot. *Plant Health Progress*, 2(1): 9. DOI: 10.1094/PHP-2001-0621-01-RV.
37. OKSANEN, J., BLANCHET, F. G. K., LEGENDRE, P., et al. (2007) Vegan: community ecology package. *Proceedings of the National Academy of Sciences*, 104: 19891–19896.
38. PERAZZOLLI, M., AZIZ, A., GRAMAJE, D., FORTES, A. M., CANTU, D. (2022) Editorial: Recent advances in grapevine–microbe interactions: from signal perception to resistance response, Volume II. Frontiers in Plant Science, 13: 1069886.
39. POITOU, X., THIBON, C., DARRIET, P. (2017) 1,8-Cineole in French red wines: evidence for a contribution related to its various origins. *Journal of Agricultural and Food Chemistry*, 65(2): 383–393. DOI: 10.1021/acs.jafc.6b03042.
40. PÕLME, S., ABARENKOV, K., NILSSON, R. H., et al. (2020) FungalTraits: a user-friendly traits database of fungi and fungus-like stramenopiles. *Fungal Diversity*, 105: 1–16. DOI: 10.1007/s13225-020-00466-2.
41. RENSINK, S., VAN NIEUWENHUIJZEN, E. J., SAILER, M. F., STRUCK, C., WÖSTEN, H. A. B. (2024) Use of *Aureobasidium* in a sustainable economy. *Applied Microbiology and Biotechnology*, 108(1): 202. DOI: 10.1007/s00253-024-13025-5.
42. ROLSHAUSEN, P. E., KIYOMOTO, R. (2012) The status of grapevine trunk diseases in the Northeastern United States. In: *Proceedings of the New England Vegetable and Fruit Conference*.
43. SAMAD, A., TROGNITZ, F., COMPANT, S., ANTONIELLI, L., SESSITSCH, A. (2017) Shared and host-specific microbiome diversity

and functioning of grapevine and accompanying weed plants. *Environmental Microbiology*, 19(4): 1407–1424. DOI: 10.1111/1462-2920.13618.
44. SIMMONS, E. G. (2007) *Alternaria: An identification manual.* Utrecht: CBS Fungal Biodiversity Centre.
45. SINGH, S. G., MEHTA, N., MEENA, P. D. (2016) *Alternaria diseases of crucifers: Biology, ecology and disease management.* Singapore: Springer. DOI: 10.1007/978-981-10-0287-0.
46. SOLDAN, R., FUSI, M., CARDINALE, M., DAFFONCHIO, D., PRESTON, G. M. (2021) The effect of plant domestication on host control of the microbiota. *Communications Biology*, 4(1): 936. DOI: 10.1038/s42003-021-02467-6.
47. TANUNCHAI, B., JI, L., SCHROETER, S. A., WAHDAN, S. F. M., LARPKERN, P., LEHNERT, A. S., et al. (2022) A poisoned apple: first insights into community assembly and networks of the fungal pathobiome of healthy-looking senescing leaves of temperate trees in mixed forest ecosystem. *Frontiers in Plant Science*, 13: 968218. DOI: 10.3389/fpls.2022.968218.
48. VANWALLENDAEL, A., BENUCCI, G. M. N., DA COSTA, P. B., FRASER, L., SREEDASYAM, A., FRITSCHI, F., et al. (2022) Host genotype controls ecological change in the leaf fungal microbiome. *PLOS Biology*, 20(8): e3001681. DOI: 10.1371/journal.pbio.3001681.
49. VARGAS CASTILLO, R., IBACETA, A., VERGARA, E. (2013) *Rinodina pyrina* (Physciaceae, Ascomycota) nueva especie para Chile. *Gayana. Botánica*, 70(2): 399–401. DOI: 10.4067/S0717-66432013000200018.
50. WHITE, T. J., BRUNS, T., LEE, S., TAYLOR, J. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: PCR Protocols: a Guide to Methods and Applications. Elsevier, 315–322. DOI: 10.1016/B978-0-12-372180-8.50042-1.
51. WU, F., FENG, Z., WANG, M., WANG, Q. (2023) Proposal of four new Aureobasidium species for exopolysaccharide production. Journal of Fungi, 9(4): 447. DOI: 10.3390/jof9040447.
52. XIE, J., MA, Y., LI, X., WU, J., MARTIN, F., ZHANG, D. (2023) Multifeature analysis of age-related microbiome structures reveals defense mechanisms of Populus tomentosa trees. New Phytologist, 238(4): 1636–1650. DOI: 10.1111/nph.18847.

PUBLICATIONS OF THE AUTHOR RELATED TO THE TOPIC OF THE DISSERTATION

Journal article:

LEPRES, L. A., MOLNÁR, A., GEIGER, A., VÁCZY, K. Z., GEML, J. (2025) Landscape-level drivers of fungal communities in grapevine, fruit trees, and semi-natural shrublands in a habitat matrix. *Plants,* 14(20): 3178.

LEPRES, L. A., MOLNÁR, A., GEIGER, A., VÁCZY, K. Z., GEML, J. (2025) A szőlő és környezete közötti fitopatogén kapcsolatok. *Növényvédelem*, 86(7): 294–303.

SPITZMÜLLER, Z., KISS, T., PÁLFI, X., **LEPRES, L. A.**, VÁCZY, K. Z. (2026) Persistent heteroplasmy of the G143A mutation in *Plasmopara viticola* populations of Hungary: Long-term maintenance of QoI resistance in the absence of selection pressure. *Physiological and Molecular Plant Pathology*: 142:103109.

Conference abstract:

MOLNÁR, A., ZSÓFI, Z., **LEPRES, L. A.**, GEIGER, A., VILLANGÓ, S., TÓTH, A. M., PÁLFI, X., LOVAS, M., BAKOS-BARCZI, N., NAGY, R., *et al.* (2025) Drought shapes fungal communities of grapevine leaves in the Eger wine region. *Abstracts of the 7th Central European Forum for Microbiology*: 52/2.

LEPRES, L. A., MOLNÁR, A., GEIGER, A., VÁCZY, K. Z., GEML, J. (2025) A szőlő és környezete közötti fitopatogén kapcsolatok = Phytopathogenic connections among grapevine and surrounding woody plants. In: HALTRICH, A. (szerk.) *Növényvédelmi Tudományos Nap 2025*: 33. Magyar Növényvédelmi Társaság.

LEPRES, L. A., MOLNÁR, A., GEIGER, A., VÁCZY, K. Z., GEML, J. (2025) Tájszintű kölcsönhatások a szőlőtermesztésben = Landscape-level microbial connections in viticulture. In: VÁCZY, K. Z., BENE, Zs. (szerk.) *Eger Wine Meetup International Conference – Research, innovation, international wine market: Program and abstract book*: 55–58. EKKE Líceum Kiadó.

LEPRES, L. A., MOLNÁR, A., GEIGER, A., VÁCZY, K. Z., GEML, J. (2025) Comparison of the core microbiome and indicator species of vineyards and surrounding Rosaceae fruit species. *Abstracts of the 7th Central European Forum for Microbiology*: 46/1.

LEPRES, L. A., MOLNÁR, A., GEIGER, A., VÁCZY, K. Z., GEML, J. (2024) Növénypatogén gombaközösségek gazdapreferenciája és szezonalitása a szőlő és a szomszédos gyümölcsösök és őshonos cserjék leveleiben és fás szöveteiben. In: DIMA, B., PAPP, V. (szerk.) *VII. Magyar Mikológiai Konferencia* – Absztraktkötet: 164–165.

LEPRES, L., MOLNÁR, A., GEIGER, A., VÁCZY, K. Z., GEML, J. (2024) DNA-based analysis of leaf and wood of grapevine, adjacent orchards and native shrubs reveal host preference and seasonality in plant pathogenic fungal communities. *International Mycological Congress IMC12 – Abstracts*, 54.

LEPRES, L., MOLNÁR, A., GEIGER, A., GEML, J. (2024) Native shrubs and fruit trees as potential inoculum sources in viticulture. *Magyar Mikrobiológiai Társaság 2024. évi Nagygyűlése / Hungarian Society for Microbiology General Meeting 2024 – Abstracts*, 17. Magyar Mikrobiológiai Társaság.

LEPRES, L., MOLNÁR, A., GEIGER, A., VÁCZY, K. Z., GEML, J. (2023) Tájszintű növényvédelem mikrobiális alapjai a szőlőtermesztésben. In: HALTRICH, A. (szerk.) *69. Növényvédelmi Tudományos Napok*, 31888796. Magyar Növényvédelmi Társaság.

LEPRES, L., MOLNÁR, A., GEIGER, A., VÁCZY, K. Z., GEML, J. (2023) Exploring the microbial connections between grapevine and nearby wild and cultivated woody Rosaceae species in the Eger wine region, Hungary. In: VERDIER, V. (szerk.) *12th International Congress of Plant Pathology – Book of Abstracts*, 291–292 (Paper P9.3-015).

GEIGER, A., LEAL, C. M., MOLNÁR, A., **LEPRES, L.**, MULLER, M., KGOBE, G., VÁCZY, K. Z., GEML, J. (2022) A szőlő növénypatogén gombaközösségére ható tényezők –mikroélőhely, fajta, egészségi állapot, évjárat, szezonalitás – vizsgálata. In: MÁRIALIGETI, K., DOBAY, O. (szerk.) *Magyar Mikrobiológiai Társaság 2022. évi Nagygyűlése: XV. Fermentációs Kollokvium*.

LEAL, C. M., GEIGER, A., MOLNÁR, A., **LEPRES, L.**, MULLER, M., KGOBE, G., VÁCZY, K. Z., GEML, J. (2022) A terroir, az évszak és az évjárat szőlő patobiomra gyakorolt hatásának vizsgálata. In: MÁRIALIGETI, K., DOBAY, O. (szerk.) *Magyar Mikrobiológiai Társaság 2022. évi Nagygyűlése: XV. Fermentációs Kollokvium*.

LEPRES, L., MOLNÁR, A., GEIGER, A., VÁCZY, K. Z., GEML, J. (2022) A szőlő és a Rosaceae családba tartozó gyümölcstermő növények gombaközösségeinek DNS-alapú összehasonlítása. In: MÁRIALIGETI, K.,

DOBAY, O. (szerk.) *Magyar Mikrobiológiai Társaság 2022. évi Nagygyűlése: XV. Fermentációs Kollokvium*.

LEPRES, L. A., GEML, J., KARÁCSONY, Z., GEIGER, A., TÁNCSIS, A., VÁCZY, K. Z. (2022) DNA-based comparison of plant pathogenic fungi between grapevine and wild woody Rosaceae with a focus on trunk diseases. *16th Congress of the Mediterranean Phytopathological Union – Book of Abstracts*, Paper 32.